The Ecology of the Nest-Building Bivalve *Musculus lateralis* Commensal with the Ascidian *Molgula occidentalis*

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(2 Plates; 3 Text figures)

POPULATION STUDY

Musculus lateralis (Say, 1822) is a small uncommon bivalve found from Delaware Bay southward throughout the Gulf of Mexico to the West Indies (Johnson, 1934). It is normally free living, attached to rocks, pilings, or any hard shallow-water substrate. It has not been reported from an ascidian.

A general bivalve-ascidian relationship has been known for over a hundred years. Jeffreys (1863) reported *Modiolaria (=Musculus) marmorata* (Forbes, 1833) from the test of *Ascidia mentula* Müller, 1776 on the coast of England. Meissner (1893) described this same species as parasitic on *Ascidiella virginea* (Müller, 1776). Bourdillon (1950, 1955) redescribed *M. marmorata* as a commensal on a number of ascidians, including *Styela plicata* (Lesueur, 1823). Aldrich (1955) reported a bivalve-ascidian relationship from the western Atlantic coast of this country. He found *Molgula manhattensis* (DeKay, 1843) attached to the protruded siphon of the clam *Mya arenaria* Linnaeus, 1758. In this case the tunicate was a hindrance to the clam because it could not withdraw its siphon into the burrow.

The host animal for *Musculus lateralis* in my study was *Molgula occidentalis* Traustedt, 1883. *Molgula occidentalis* is found in abundance on the sand-mud substrate in shallow water from Cape Cod throughout the Gulf of Mexico and the West Indies to Brazil. It is present, and easily collected, in the study area, a protected shallow bay, Alligator Harbor, Franklin County, Florida. *Molgula occidentalis,* although a simple ascidian, is usually found growing in clumps of 3 to 15 in this area. Because of its size and secure attachment in the soft substrate, it attracts many organisms seeking shelter and protection. One of these is the bivalve *Musculus lateralis.*

The population sample in this study was based on 50 specimens of *Molgula occidentalis* taken in Alligator Harbor at a depth of 2 - 3 meters in March, 1967. The bivalves were removed from the tunicate with a probe and the total length measured to the nearest millimeter with an ocular micrometer. *Musculus lateralis* was present on 37 of the 50 specimens (Figure 1). A total of 412 were recorded with an average of 11.1 for the 37 tunicates with *Musculus.* The range in numbers was 0 to 48. Of the 412 taken, 389 were measured. Those not measured had both valves chipped or broken when removed from the tunicate. The size range was 2 to 9 mm and the average size was 6.7 mm.

An earlier collection of 35 *Molgula occidentalis* was dredged off Turkey Point in Franklin County, Florida in December, 1966, at a depth of 5 - 6 m. A third collection of *Molgula,* composed of 65 live beach specimens, was made after a storm in March, just east of the Florida State Marine Laboratory at Alligator Harbor. The specimens of *Musculus lateralis* from these two collections were counted and recorded, but not measured. A collection of 12 *Styela plicata* was dredged in Alligator Harbor in March, and another of 100 was made from a float at the end of the dock at the marine laboratory. The *Musculus lateralis* on these specimens were also counted and recorded, but not measured. One specimen of *S. plicata* from Turkey Point was also obtained and checked.

The 35 specimens of *Molgula* from the Turkey Point collection yielded 1487 *Musculus lateralis* for an average of 42.4 per tunicate. The range was from 17 to 77 (Figure 2). All of the tunicates had *Musculus* present. From 65 *Molgula occidentalis* picked up alive on the beach in Alligator Harbor, there were no *M. lateralis.* Of the *Styela plicata* examined, the 12 specimens from Alligator Harbor yielded 174 *Musculus* for an average of 14.5 per tunicate. The range was 4 to 30 (Figure 3). The single Turkey Point specimen yielded 90 *M. lateralis.* The 100 specimens taken from the float at the end of the dock had no *Musculus* attached.

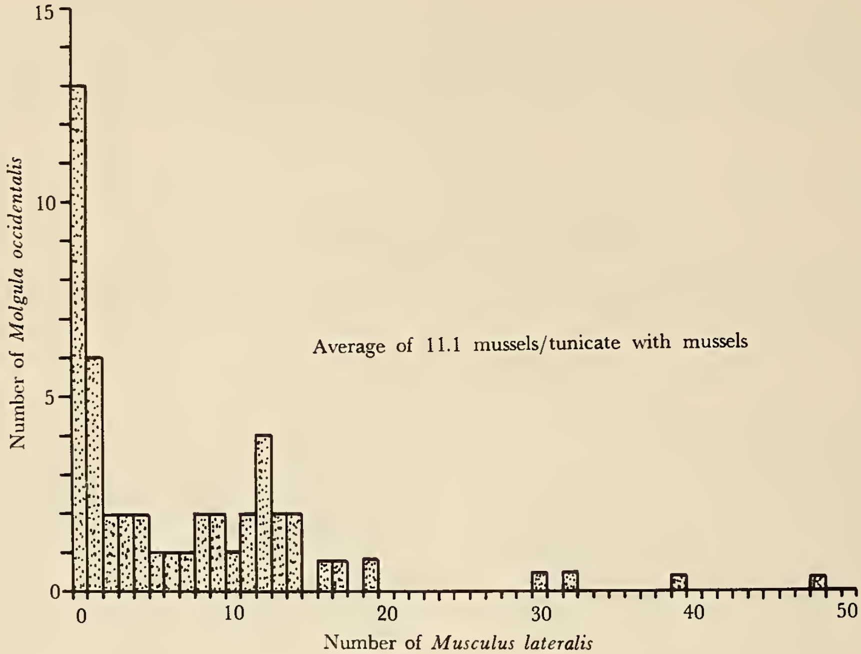

Figure 1

The distribution of *Musculus lateralis* on *Molgula occidentalis* from the Alligator Harbor Collection of March, 1967

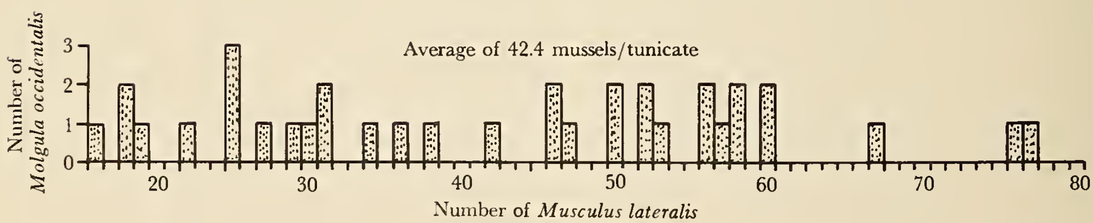

Figure 2

The distribution of *Musculus lateralis* on *Molgula occidentalis* from the Turkey Point Collection of December, 1966

DISCUSSION

If *Musculus lateralis* is present at all on *Molgula occidentalis,* it is usually there in abundance. The explanation for this can be arrived at by an examination of its mode of reproduction. This species and other members of the genus lay egg-strings on the inside of a prepared nest. Here the eggs hatch and develop without leaving the nest. The postlarvae remain in or near the nest, feeding from the parental currents (Merrill & Turner, 1963; MacGinitie, 1955; Ockelman, 1958). As in the case of many organisms that care for the young, the eggs are large and few in number (Thorson, 1935). If the bivalve secures a place to build a nest on the tunicate, it is in a position to increase its numbers quickly. If the tunicates are attached in a clump, and mussels are on one tunicate, they are likely to be on all tunicates.

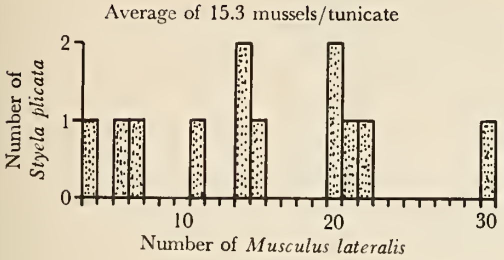

Figure 3

The distribution of *Musculus lateralis* on *Styela plicata* from the Alligator Harbor Collection of March, 1967

Musculus lateralis is usually a hard-bottom dweller and its mode of reproduction keeps it from colonizing new areas rapidly. A clear area of sand or a distance of open water can prevent it from inhabiting certain new areas. The float from which the 100 specimens of *Styela plicata* were taken was one of these areas. The tunicate larvae are pelagic and grow rapidly after attachment (GRAVE, 1936; BERRILL, 1950). The adult tunicates on the float had not yet been reached by *Musculus* nor many of the epifaunal organisms.

The 65 beach specimens came from an area just east of the marine laboratory. This area is very sandy and the epifauna is scarce. *Molgula occidentalis* larvae can settle in this area on a small shell fragment or any small hard particle. Their tenuous position is evidenced by their washing ashore during a storm. All 65 ascidians examined were solitary, that is, not attached to other *Molgula*. Like the *Styela* on the float, they were free of *Musculus lateralis.*

Conversely, those individuals living in a sand-mud substrate had a large number of *Musculus lateralis* attached. The individual tunicates from Turkey Point were attached to each other in clumps of from 2 to 10. These yielded the largest total number of *Musculus,* with a high average number per tunicate. The greater depth of water, lesser turbidity, greater concentration of nest-building materials, and what appeared to be a larger average size of the tunicates, probably contributed to the greater concentration of mussels on the tunicates.

BOURDILLON (1955) found that the number of *Modiolaria marmorata* (which is about the same size as *Musculus lateralis*) on *Styela plicata* varied greatly between individuals. The largest number of *Modiolaria* he found in a single *Styela* was 61. The largest number found in my study was 90. His count was made from a tunicate 5 cm long, whereas the Turkey Point specimen used here was about 8 cm long. The percent of tunicates from Bourdillon's study that contained *Modiolaria* varied from 5 to 100%, in the present analysis from 0 to 100%.

NEST BUILDING

Many species of bivalves attach themselves to solid objects by means of a byssus, but in the family Mytilidae it is most fully developed. WHITE (1937) described in detail the process by which byssal threads are formed in *Mytilus edulis* Linnaeus, 1758. The foot has a posterior groove continuous with the byssal aperture. The groove itself and special byssal glands at their base secrete a substance called conchiolin. The conchiolin flows down the groove which terminates in a sucker. The sucker itself secretes a cement which adheres when placed in contact with the substrate. The groove opens and the conchiolin thread, on exposure to sea water, hardens.

The formation of these threads is usually confined to spinning a byssus, a strong band composed of many threads, but some species have developed the ability to weave these threads into a protective covering or nest. Robertson described this type of nest building of *Lima hians* (Gmelin, 1791) in JEFFREYS, 1863, as did GILCHRIST (1897). JOHNSON (1931) did the same for *Lima inflata* Lamarck, 1819. HAAS (1942, 1943) described the nest of *Diplodonta orbella* (Gould, 1851) and *Cooperella subdiaphana* (Carpenter, 1864) as being composed primarily of sand adhering to mucus. Thus, this latter type of nest is not composed of threads as is that of *L. hians.* Instead, a large ball of mucus forms at one end and gradually accumulates particles. The volume of mucus increases until the bivalve is successfully camouflaged.

MACGINITIE (1959) described the nest of *Musculus discors* (Linnaeus, 1767) from the coast of Alaska. The nest-building of this species was later described from laboratory observations by MERRILL & TURNER (1963). This nest proved to be of the former type or a thread nest. As yet, no one has described the nest, or followed the nest building, of *M. lateralis.*

LABORATORY OBSERVATIONS

In March, 1967, 50 live specimens of *Musculus lateralis* were removed from their nest of *Molgula occidentalis* and placed in aquaria in running sea water at the Florida State Marine Laboratory. The bivalves were put into glass petri dishes which were suspended in the aquaria in a wire net fashioned of stainless steel. Additional petri dishes with new *Musculus* were added in the course of the experiment to obtain a comparison of old and new nests. The water temperature during the experiment fluctuated between 19 and 25° C. The flow of water into the aquaria remained relatively constant except for one 12 hour period and one 4 hour period in which the salt water pump failed. The aquaria were not lighted at night except during occasional checks on nest building when indirect lighting was used.

Like most mytilids that secrete a byssus, the first action of *Musculus lateralis,* when put in a new environment, was to secrete a few threads to secure an attachment to the substrate. This was done within the first 2 hours for 44 of the 50 specimens in the aquaria (Figure *4*). Those that did not initially secrete a byssus usually did not complete a nest and subsequently died.

The specimens were placed during daylight, either in late morning or early afternoon; consequently, once the initial threads were out, activity ceased until dark. After putting out the initial threads, *Musculus lateralis* proceeded to build the nest in the following fashion. First, a ball of mucus formed at the posterior end of the specimen. As the threads were formed, drops of the mucus stuck to them. This feature made it easy to detect the newly formed threads. In the aquaria each bivalve initiated building while lying on its side on one valve. The foot extended and attached a series of threads directly in front of the anterior margin of the valves. After 15 to 20 threads were in place, the foot reached over the top valve and attached another series to the floor of the petri dish on the opposite side (Figure *5*). During the 10-hour period in which weaving took place on the first day, about 40 strands were attached. The placement of these threads over the top valve tended to lift the mussel more into an upright position at about 30° from the horizontal. With further building, some individuals completely righted themselves and were positioned on the dorsal surface, while others remained on one valve in the completed nest. The second day each mussel continued putting out threads in a radial manner until the shell was completely surrounded by threads radiating from the byssal aperture. At this point there were about 100 threads surrounding the shell (Figure *6*). After this basic pattern of the nest was formed, the mussel began secreting longer threads farther away from the shell and reinforcing the already existing threads. At this point the mussel seemed to be enclosed in a tent with the shell margin acting as the top ridge. The threads themselves were not connected to the shell in any way, but to the byssal aperture. When the valves were open for feeding, the byssal retractor muscle and the anterior and posterior adductors were relaxed. The byssal aperture was raised dorsally toward the margin of the shell and the threads were loose. Upon closing, the byssal retractor pulled the aperture back and with it the threads of the nest. The valves closed and the nest tightly covered the shell.

At the end of a week the nest was composed of about 250 threads. The threads themselves, when first secreted, were almost transparent. They were extremely thin but strong. As the threads hardened, the color changed from transparent to yellow and then to brown. The appearance of the nest at this time changed considerably. Sand, detritus, algae, and other organisms began to accumulate on and in the nest network. In one instance a piece of shell material 2 mm long was incorporated into the nest. At any time from 3 to 4 weeks the bivalve became completely hidden within the nest (Figure *7*). All the while, *Musculus lateralis* added new threads to the nest, but the progress was slower. The weaving was intermittent and threads were not added every night.

Each specimen building a nest on the vertical wall of the petri dish followed the same pattern as the others except that, because of its position (dorso-ventral with one valve against the glass) it secreted a larger number of threads on the dorsal side before going over the outer valve to secure threads underneath.

The threads of one specimen did not attach in any way to its own shell, but this was not so of other shells. Three specimens in close proximity built their nests in an overlapping fashion with the threads of one attached to the petri dish and to other shells. The nests so constructed formed an intertwining network which covered the group completely. The shells within the nests were undetectable after 3 weeks except when the mussel was feeding.

Except for feeding and nest building, the valves remained closed. During daylight for the nearly two months the organisms were kept in the aquaria, only one individual was seen in any activity other than feeding. This specimen was not one from the petri dishes, but one previously placed on the bottom of a 5-gallon capacity aquarium. It moved across on the bottom and climbed the vertical side of the aquarium to a height of 8 inches. In this position it put out a series of threads to secure attachment and then ceased movement.

The foot of *Musculus lateralis* is quite remarkable. When fully extended, it is longer than the specimen itself. When first observed, the foot looks like a cream-colored nematode leaving the bivalve. This foot is extremely flexible as was evidenced by the manner in which the bivalve climbed the aquarium glass. The foot, like that of *M. discors,* is equipped with a pedal disc which can attach a byssal thread when placed against the substrate. During

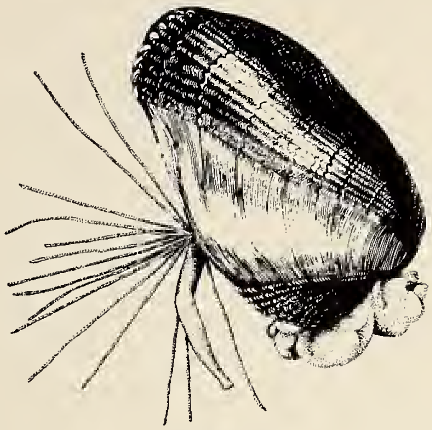

Figure *4*

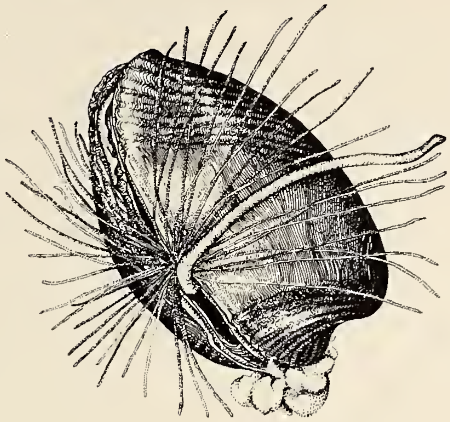

Figure *5*

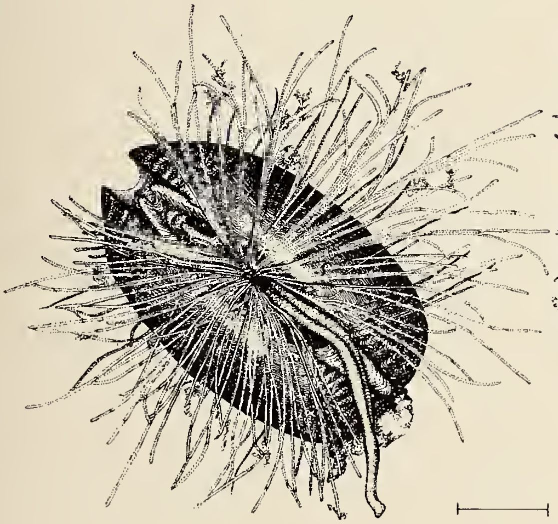

Figure *6*

Figure *7*

The Nest Building of *Musculus lateralis*

Figure *4*: 2 hours Figure *5*: 24 hours Figure *6*: 2 days

Figure *7*: 1 week

Bar is 1 cm long

horizontal movement along a flat surface the foot is extended ahead of the bivalve, attaches, and on contraction pulls the valves up to the new position. This is done without the secretion of any byssal thread. To move vertically on the glass, the foot is extended, attached, and the body of the shell drawn up. A thread is then secreted and the shell is suspended while the foot extends to its maximum length and attaches again. The shell is again drawn upward with the byssal thread either being broken or released. With this manner of movement, the bivalve was able to move the distance in a matter of minutes. Although this specimen was the only one observed in motion, several others managed to negotiate the distance. One specimen made the trip on 4 successive nights after being replaced on the bottom each day.

If the *Musculus* are open, the gap of the valves is wide and very noticeable. When the *Molgula* are first collected, the *Musculus* valves tend to gape and the number of bivalves can be counted.

FIELD OBSERVATIONS

The process of nest building by *Musculus lateralis* on *Molgula occidentalis* in the field is the same as in the laboratory, but the result is different for the following reason. The body of the shell, either partly or completely, is impressed into the test of the ascidian. The older the ascidian grows and the longer *Musculus* is embedded, the shorter the distance to the edge of the indentation becomes. Thus, the early nest material piles up on the top and sides of the outward oriented shell margin. This network provides protection and shelter for a myriad of small invertebrates. Nests of larger specimens taken in the field appear to have no symmetry or pattern as do the newer nests fashioned in the laboratory. The "bump" that appears on the outside of the test denoting the presence of a single bivalve on a small surface is entirely missing when a large number of intertwining *Musculus* is present. The nests blend together to form a mat-like effect and a generally even surface results.

Although the bivalve is embedded in the test, it does not break the strong cuticle covering the test. Instead, the flexible cuticle is pushed inward until a depression is formed. When the bivalve closes its shell, the threads become tight and exert a downward pressure on the shell. Through this pressure and friction of movement within the nest, the cuticle is gradually pushed into the test until the depression is made. These depressions are permanent in that they remain when the mollusk is removed. It was observed that the depression under dead valves was not as deep and the cuticle seemed to be returning to normal through growth. This was especially true in the top third of the test surrounding the siphons. In this area the test was several millimeters thick, but was composed of the same milky cellulose material that made up the remainder of the test. In this area some indentations caused by *Musculus* were up to 5 mm deep from their lip. Small (2 - 3 mm in diameter) whitish circles scattered randomly on the inside of the test could be seen when the test was inverted. These "scars," at the base of the embedded *Musculus,* were most noticeable on the ventral two-thirds of the test where it was thin, but they were discernible even in the thickened anterior portion. A few spots were seen where no *Musculus* were embedded and the exterior of the test appeared normal. From these scars the past presence of a bivalve or some attached foreign object can be deduced.

While almost all of the larger specimens were found in nests, small mussels (2 mm or less) did not build nests of their own, but lived within the nest of an adult, feeding from the water currents created by it. This is not strange in view of the reproductive habits of *Musculus.* During the entire study, two adults were never taken from the same nest.

DISCUSSION

The question of how *Musculus lateralis* comes to lie embedded in the tunic of *Molgula occidentalis* is important because it could indicate the presence or absence of host specificity. Bourdillon (1950) stated from experimental evidence that *Modiolaria marmorata* became embedded in the test of *Styela plicata* because of its chemical attraction to the cellulose nitrates which compose the test. Thus, the attraction to the tunicate would be primarily a chemical one. He further stated that the mechanical stimulus of the water currents created by the tunicate played no part in the attraction.

In a later paper (Bourdillon, 1955) he reversed the earlier proposals and said the attraction of the bivalve to the tunicate was due entirely to the mechanical attraction to the test because of its consistency as a substrate for inclusion. He also reaffirmed his position that the water currents produced by *Styela plicata* played no part in the attraction.

As was previously stated, *Styela plicata* is abundant in Alligator Harbor and is used by *Musculus lateralis* as a substrate for embedding and nest building. *Musculus lateralis* embeds in *Styela* in a wide band composing the middle third of the elongated test. In this position it can